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ORIGINAL ARTICLE

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Impacts of nitrogen-fixing and non-nitrogen-fixing tree species on soil respiration and microbial community composition during forest management in subtropical China

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Abstract Forest management with N-fixing trees can improve soil fertility and tree productivity, but have little information regarding belowground carbon processes and microbial properties. We aimed to evaluate the effects of three forest management regimes, which were *Erythrophleum fordii* (N-fixing tree), *Pinus massoniana* (non-N-fixing tree), and their mixed forest, on soil respiration and microbial community composition in subtropical China, using Barometric Process Separation and phospholipid fatty acid profiles, respectively. We found that the inclusions of N-fixing species in forests significantly increased the soil respiration, but have no effects on SOC and ecosystem total C stock. In addition, soil microbial communities were obviously different among the three forest management regimes. For instance, total and bacterial PLFAs were higher in the *E. fordii* and mixed forest than in the *P. massoniana* forest. Conversely, fungal PLFAs in the *P. massoniana* forest were elevated versus the other two forests. Soil total N, nitrate-N and pH were the key determinants shaping the microbial community composition. Our study suggests that variations in soil respiration in the studied forests could be primarily explained by the differences of root biomass and soil microbial biomass, but not soil organic carbon. Although soil fertility and microbial biomass were promoted, N-fixing plantings also brought on increased CO_2 emissions in laboratory assays. The future decision of tree species selection for forest management in subtropical China therefore needs to consider the potential influences of tree species on CO_2 emissions.

Keywords Soil respiration · Microbial PLFAs · Microbial community composition · N-fixing tree species · Forest management regimes

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Introduction

Soils are the largest reservoir for carbon (C) in terrestrial ecosystems (Raich and Schlesinger 1992). The emission of carbon dioxide (CO_2) from soils through autotrophic and heterotrophic respiration is recognized as one of the largest fluxes and plays an important role in the global C cycling (Schlesinger and Andrews 2000; Janssens et al. 2001). Soil respiration has been shown to be sensitive to climate, vegetation composition, land-use changes, and soil types (Brüggemann et al. 2005; Epron et al. 2006; Shi et al. 2015a). Changes in forest management regimes can substantially alter soil organic C (SOC) dynamics and affect soil-atmosphere exchanges of CO_2 by changing tree species composition that influence litter's quality and quantity, decomposability of organic matter, root system, and microbial activity (Janssens et al. 2001; Tang et al. 2006; Sheng et al. 2010; Wang et al. 2010a; Vesterdal et al. 2013; Yuan et al. 2013). Thus, tree species selection in forest management and planting regimes is closely related to the exchanges of CO_2 between soil and atmosphere.

Microorganisms are treated as decomposers in soils, that utilize organic matter primarily derived from above- and belowground litters, root exudates, woody debris and animal remains as their C sources. Soil microorganisms have also been shown to play a unique role in the processes of nutrient cycling and C and N turnover

(Huang et al. 2014). In soils, it has been proposed that the growth and activity of soil microorganisms is limited by the substrate availability, especially for C availability (Griffiths et al. 1998). Entry of organic matter into the soil is therefore considered to be a key factor which regulates the soil microbial community composition (Griffiths et al. 1998). In terrestrial ecosystems, a significant portion of soil organic matter (SOM) is respired by microbes to generate energy for cellular processes (i.e., microbial catabolic metabolism) or is assimilated into soil microbial biomass (i.e., microbial anabolic metabolism) (Keiblinger et al. 2010). As a result, soil microbial communities would shape the effectiveness and mechanisms of utilizing SOM by microbes (Balser and Wixon 2009; Keiblinger et al. 2010). The size and composition of soil microbial community may thus affect the SOM decomposition and CO_2 production. In addition, variations in N availability also determine the soil microbial biomass and community structure (Ushio et al. 2008; Cao et al. 2010). Previous studies have shown that higher soil N availability or lower C/N ratio may favour bacterial decomposers over fungal decomposers (Lundquist et al. 1999; Williamson et al. 2005). Moreover, soil fungi generally are the primary decomposers of recalcitrant organic compounds, whereas bacteria are more efficient in coping with simple carbohydrates, organic acids, and amino acids than fungi (Myers et al. 2001; Hackl et al. 2005). Therefore, increased substrate N availability may shift the soil microbial community towards bacterial dominance, slowing the decomposition of recalcitrant organic matter and increasing the soil C sequestration. Changes in forest management regimes are accompanied by changes in tree species composition and stand structure, and subsequently changes in soil physiochemical properties and substrate's quality and quantity. A large amount of work has been conducted to study the effects of forest vegetation composition on soil microbial community structure (Hackl et al. 2005; Högberg et al. 2007; Wagai et al. 2011; Lucas-Borja et al. 2012). These studies have underlined the importance of the substrate's quality and quantity as well as abiotic factors (e.g., soil temperature, moisture, bulk density, pH and texture, etc.) to the soil microbial community. Soil microbial properties can therefore be considered as potential indicators to determine the influences of forest management regimes on soils.

In order to satisfy the increasing requirements for forest products while avoiding excessive harvesting of natural forests, plantations have been rapidly expanding as a major component of forest resources in the world and playing a key role in sustainable forest management (Wang et al. 2010a; Huang et al. 2014). Multi-objective and well-designed plantations do not only reduce the logging pressure on natural forests and keep some ecological service functions provided by natural forests, but also have a profound effect on the ecosystems' C sequestration (Paquette and Messier 2009). In areas of subtropical China, commercial forests are extensively managed through afforestation and reforestation. However, the large-scale selection and planting of single coniferous tree species (e.g., *Pinus massoniana* and *Cunninghamia lanceolata*) or exotic tree species (e.g., *Eucalyptus*) has caused a series of ecological problems, such as the reduction of soil fertility, loss of biodiversity and poor stability of ecosystem (Carnevale and Montagnini 2002; Liang 2007). Nitrogen-fixing tree species (e.g., *Erythrophleum fordii* and *Acacia mangium*) have been widely used for mitigating soil nutrient deficiency and site degradation due to their N-fixing capacity during forest management in subtropical China. It has been proposed that mixed-species management regimes with N-fixing trees are likely to improve plantation yields (Binkley et al. 2003; Forrester et al. 2004, 2006a), soil fertility (Forrester et al. 2006b; Wang et al. 2010b; Huang et al. 2014), and C sequestration (Johnson and Curtis 2001; Resh et al. 2002; Hoogmoed et al. 2014a; Shi et al. 2015b). However, to our knowledge, few reports are available on belowground microbial characteristics regarding N-fixing trees for forest management (Boyle et al. 2008; Bini et al. 2013; Hoogmoed et al. 2014b; Huang et al. 2014), and there appears to be no consistent trends in soil microbial biomass and community structure. Soil microbial community composition has been shown to be significantly different between N-fixing (*A. mangium*) and non-N-fixing (*E. urophylla*) plantations, and soil microbial biomass C has seemed to be obviously higher in plantations of *A. mangium* than *E. urophylla* (Huang et al. 2014). In contrast, there was no significant difference in microbial community composition between N-fixing and non-N-fixing plantings, such as *Alnus rubra* vs. *Pseudotsuga menziesii* (Boyle et al. 2008); *A. dealbata* vs. *E. camaldulensis* (Hoogmoed et al. 2014b) or in microbial biomass C or N under *A. mangium* compared with *E. grandis* plantations after 20 months' planting in Brazil (Bini et al. 2013). Further, little is known about the impact of microbial signature phospholipid fatty acids (PLFAs) on belowground C dynamics in forest soils. In a few related studies, there were some connections between soil respiration and the concentration of the PLFA 16:0 and the ratio of gram-negative to gram-positive bacteria PLFAs (Wang et al. 2013).

Understanding the response of soil microbial communities to N-fixing and non-N-fixing plantings has important implications for the restoration of soil fertility and reestablishment of soil microbial ecological function. Furthermore, determining the biological mechanisms controlling belowground C processes is essential to predict the changes of soil C sequestration in response to changes of forest management regimes. Here we conducted a field-based study to compare the soil respiration and microbial community composition in monoculture and mixed plantations of N-fixing and non-N-fixing tree species in subtropical China. The purposes of this work were (1) to explore how soil respiration and microbial community composition changed with distinct forest management regimes, and (2) to identify which soil properties were the significant drivers for the variations in microbial community composition.

Materials and methods

Site description

The study site (106°42′E, 22°10′N, 120–210 m asl, 10° slope) is situated at the Experimental Center of Tropical Forestry, Chinese Academy of Forestry, Pingxiang City, Guangxi Zhuang Autonomous Region, P.R. China. The selected site is representative of the regional features of afforestation and reforestation in southern China. This region experiences a typical subtropical monsoon climate with an annual average temperature of 21.0 °C and relative humidity ranging from 80 to 84 %. Annual mean rainfall is ~1400 mm, occurring intensively during the period of April to September and annual evaporation averages 1261–1388 mm per year. The soils at the study area is formed from weathered granite and classified as lateritic red soil in the Chinese system of soil classification, which is equivalent to an oxisol in the USDA Soil Taxonomy (State Soil Survey Service of China 1998; Soil Survey Staff of USDA 2006).

Three plantations with different tree species composition were chosen for sample collection representing three different forest management regimes: a monoculture of *E. fordii* forest, a monoculture of *P. massoniana* forest, and a mixed plantation composed of *E. fordii* and *P. massoniana*. Historically, this area was vegetated with a single coniferous species, *P. massoniana*; seedlings were planted in 1983 on a deforested hill. In 2006, the current plantations with the same density of 2500 trees hm^{-2} were designed after clear-cutting of the *P. massoniana* plantation to compare the tree productivity in short-rotation forests of contrasting management regimes. *E. fordii* and *P. massoniana* are main indigenous tree species used for afforestation and reforestation in this area. *E. fordii* is a leguminous N-fixing species well-adapted to the local soil conditions and the subtropical climate. The configuration of the mixed forest is 1:3 (i.e., 25 % *E. fordii* + 75 % *P. massoniana*). The undergrowth vegetation is mainly characterized as *Lygodium japonicum*, *Dicranopteris dichotoma*, *Cyrtococcum patens*, and *Lophatherum gracile*.

Soil, litterfall and fine root sampling

Three replicate field sites were selected for sampling in each of these three forest management regimes (i.e., 9 field sites in total). Seven soil cores were randomly collected from each sampling site at a depth of 0–10 cm using a stainless soil corer (6-cm diameter) in May 2013. The seven soil cores from each sampling site were composited as a homogeneous and representative sample and thus pooled to yield three composite samples per plantation. During sampling within each site, the corer was wiped clean of obvious soil particles with paper towels. After the soil was sieved through a 2 mm mesh to remove visible roots, stones, plant debris, and soil animals, all samples were placed in polyethylene bags in duplicate and immediately transported to the laboratory. One was air-dried and sieved using a 0.25 mm mesh for soil properties analysis, and the other was stored at −20 °C prior to PLFA analysis.

Seven litter fall-traps (each of 1 m × 1 m) with a mesh size of 1 mm were placed about 1 m above the ground surface at each site (Wang et al. 2010a). Litterfall was collected monthly from September 2012 to August 2013. Litterfall samples were oven dried at 70 °C until a constant weight was achieved and a subsample was used for C and N analysis. Fine root (diameter < 2 mm) biomass was investigated using sequential soil coring method (Hertel et al. 2009). From September 2012 to August 2013, seven soil cores from the upper 20 cm of the soil were taken from each site monthly with a stainless soil corer (6-cm diameter). The fine root samples were subsequently picked up and oven dried at 70 °C until a constant weight. A fine root subsample was used for C and N analysis. The fine root biomass was estimated by the average of fine root biomass of the 12 sampling times.

Soil, litterfall and fine root chemical analysis

Soil, litterfall and fine root chemical properties were measured according to the procedures described by Lu (2000). Organic C was determined using potassium dichromate oxidation and titration with ferrous ammonium sulfate. Total nitrogen (TN) was analyzed by micro-Kjeldahl digestion (UK152 Distillation & Titration Unit, Italy). The C/N ratio was calculated as the ratio of organic C to TN. Soil samples were extracted with 2 M potassium chloride (KCl) solution, and ammonium-N (NH_4^+-N) and nitrate-N (NO_3^--N) in extracts were determined with a flow injection auto-analyzer (FIA, Lachat Instruments, USA). Soil pH was measured using a 1:2.5 mixture of soil:deionized water suspension.

Soil temperature, moisture and soil respiration

The in situ soil temperatures 5 cm below the soil surface were measured using a digital thermometer. Soil moisture (0–10 cm) was estimated by the relative water content as the percentage of water-filled pore space (WFPS). Soil water content and bulk density were determined gravimetrically by drying the soil samples at 105 °C for 24 h. Soil WFPS was calculated based on the following formula (Franzluebbers 1999): WFPS = (SWC × BD)/[1 − (BD/PD)], where SWC is the soil water content ($g\ g^{-1}$), BD stands for soil bulk density ($g\ cm^{-3}$), and PD denotes the soil particle density, which was assumed to be 2.65 $g\ cm^{-3}$.

Soil respiration was measured using a Barometric Process Separation (BaPS) instrument (UMS GmbH Inc., Germany) through laboratory incubations as described by Ingwersen et al. (1999). From September 2012

to August 2013, seven intact soil cores were randomly collected from each sampling site bimonthly. The soil cores were sealed with parafilm and transported at coolers to the laboratory after sampling, where they were processed immediately. The BaPS system has a container holding a maximum of seven soil cores introduced to determine soil respiration, nitrification and denitrification. BaPS technique is based on the measuring of air pressure and oxygen (O_2) and CO_2 concentrations in an airtight vessel by incubating an intact soil core. In such an isothermal, gas-tight, closed system, the processes of soil respiration, nitrification and denitrification are the only relevant processes responsible for the changes of gas pressure. Based on the total gas balance and inverse-balancing approach, the rates of soil respiration, nitrification and denitrification can be mathematically calculated. Briefly, the seven intact soil cores were incubated in parallel in an isothermal water bath at temperatures characteristic of those measured in the field. After temperature equilibration, the top of the container was closed gas tight by means of a container lid, into which (1) a pressure sensor for the continuous record of air pressure changes within the gas-tight closed system, (2) a Vaisala probe for the measurements of air temperature and relative humidity, and (3) a gas-sampling port for the removal of gas samples from the headspace above the soil core were inserted. Prior to experiments, gas tightness of the incubation system containing the soil cores was tested. The incubation time for the soil cores in the closed system was typically 12 h. The data were recorded on a PC using a data acquisition system. For well-aerated soil samples, this method is a time-saving and easy-to-apply alternative that allows for minimizing any soil perturbation. Moreover, the rates of soil respiration, gross nitrification and denitrification can be determined simultaneously. For further details about the BaPS technique and relevant measuring processes see Ingwersen et al. (1999), Müller et al. (2004), Brüggemann et al. (2005), Chen and Huang (2006), and Rosenkranz et al. (2010). Previous studies have shown good agreement in the result of soil respiration measured by BaPS and gas chromatography (GC) (Liu et al. 2005).

PLFA analysis

Soil microbial community composition was assessed by the phospholipid fatty acid (PLFA) profiles (Frostegård and Bååth 1996; Bossio et al. 1998). Briefly, triplicate fresh soil equivalent to 8 g dry weight were extracted for 2 h using 23 mL of chloroform:methanol:phosphate buffer (1:2:0.8). The chloroform layer was decanted and dried under N_2 at 32 °C. The extracts were sequentially fractionated into neutral lipids, glyceride, and phospholipids using chloroform, acetone, and methanol using silica gel-filled solid-phase extraction cartridges. The samples were then subjected to mild alkaline methanolysis by dissolving them in 1 mL of methanol:-toluene (1:1) and 1 mL of 0.2 mol L^{-1} KOH, and heating them at 37 °C for 15 min. Subsequently, 2 mL of H_2O and 0.3 mL of 1.0 mol L^{-1} acetic acid were added. The resulting fatty acid methyl esters were separated, quantified, and identified by GC (N6890, Agilent, USA) fitted with a MIDI Sherlocks microbial identification system (Version 4.5, MIDI, USA).

For each soil sample, concentrations of each PLFA were calculated based on the methyl nonadecanoate (19:0) internal standard concentrations. Bacterial signatures were identified by the following PLFAs: i14:0, i15:0, a15:0, 15:0, i16:0, 16:1ω7c, 17:0, i17:0, a17:0, cy17:0, 18:1ω7c and cy19:0. We calculated the sum of PLFAs i14:0, i15:0, a15:0, i16:0, i17:0 and a17:0 as the gram-positive bacteria, and the sum of PLFAs 16:1ω7c, cy17:0, 18:1ω7c and cy19:0 as the gram-negative bacteria. The PLFAs 18:1ω9c and 18:2ω6,9c were used as indices for fungi, and PLFA 16:1ω5c was used as a marker for arbuscular mycorrhizal fungi (AMF). Actinomycetes were identified using the PLFAs 10Me16:0 and 10Me17:0 (Frostegård and Bååth 1996; Zelles 1997; Bååth and Anderson 2003). Other PLFAs such as 14:0, 16:0, 18:0, 16:1 2OH, 16:1ω9c, 17:1ω8c and cy19:0ω8c were also used to analyze the microbial community composition. All of the PLFAs indicated above were considered to be representative of the total PLFAs of the soil microbial community.

Statistical analysis

Soil, litterfall and fine root chemical properties and microbial variables were analyzed using one-way analysis of variance (ANOVA) to evaluate statistical differences among the forest management regimes. Repeated measures ANOVA was used to examine the effects of forest management regime, sampling time, and their interactions on soil respiration. Data were natural-log or square root transformed when necessary to meet assumptions of normality and homogeneity of variance. All statistical tests were performed using SPSS 19.0 (SPSS Inc., Chicago, USA). Significant differences were set as $P < 0.05$. PLFA biomarkers obtained from the sampled soils were standardized before performing principal component analysis (PCA) to ensure each PLFA had the same weight in the analysis. Redundancy analysis (RDA) was used to analyze the responses of soil microbial community composition to chemical properties using CANOCO software (version 4.5, Microcomputer Power, Inc., Ithaca, NY) for Windows. Automatic selection of means by Monte Carlo permutations was used to test the significance of the variables ($P < 0.05$). Additionally, Pearson's test was used to analyze the relationships between the microbial PLFAs and the soil chemical properties, as well as the soil respiration and microbial PLFAs. Figures were generated using SigmaPlot version 10.0.

Results

Soil, litterfall and fine root chemical properties

Significant differences were found among the three forest management regimes for all soil, litterfall and fine root chemical properties except for SOC and fine root C/N ratio (Table 1). The concentrations of TN, NH_4^+-N, and NO_3^--N tested from the *E. fordii* and mixed forest were significantly higher than those in the *P. massoniana* forest. In contrast, soils from the *P. massoniana* forest had the highest C/N ratio and pH. The highest concentration of SOC was detected in the *E. fordii* forest which was 6.6 % higher than in the mixed forest and 10.1 % higher than in the *P. massoniana* forest, respectively, though differences among these three forest management regimes were not significant. The litterfall and fine root biomass, litterfall N and fine root C contents of the *E. fordii* and mixed forest were significantly higher compared with those of the *P. massoniana* forest. However, the litterfall C/N ratio of the *E. fordii* and mixed forest was significantly decreased by 46.7 and 61.5 %, respectively, relative to that of the *P. massoniana* forest. In addition, there were no significant differences in ecosystem total C stock among these management regimes.

Soil temperature, moisture and soil respiration

Soil temperature and WFPS measured from all forest management regimes exhibited notable seasonal variations, with the highest values being observed in September 2012 (the hot-humid season) and lowest values in January 2013 (the cool-dry season) (Fig. 1a, b). The sampling time in November 2012 was a particularly shorter wet episode in the cool-dry season. Considering the historical climatic conditions in this region, November 2012 was included in the cool-dry season. There were no significant differences in soil temperature and WFPS among forest management regimes within each sampling time.

Soil respiration measured from all forest management regimes also displayed a significant seasonal variation, which was lower during the cool-dry season (from November 2012 to March 2013) compared with the hot-humid season (September 2012, May 2013, and July 2013) (Fig. 1c). Soil respiration varied between 2.3 and 25.9 mg C kg^{-1} soil dry weight (SDW) day^{-1} in the three forest management regimes during the whole study period. There were significant forest management regime and sampling time effects on soil respiration. The soil respiration in the *E. fordii* and mixed forest was 31.0 and 10.3 % significantly higher than that in the *P. massoniana* forest, respectively.

The dynamics of soil respiration in all forest management regimes coincided with those of soil temperature and WFPS (Fig. 2). When each forest management regime was considered independently, soil respiration was significantly correlated with soil temperature and WFPS. The response of soil respiration to temperature could be well described with the exponential function ($R^2 = 0.817–0.895$, $P < 0.001$). Meanwhile, we found a linear relation between soil respiration and WFPS ($R^2 = 0.287–0.336$, $P < 0.05$).

Soil microbial PLFAs

The soil microbial biomass (represented by microbial PLFAs) of total, bacteria, actinomycete, AMF, gram-

Table 1 Soil, litterfall and fine root chemical properties measured from the three forest management regimes

Chemical properties	*Erythrophleum fordii* forest	Mixed forest	*Pinus massoniana* forest
Soil organic carbon (SOC, g kg^{-1})	18.80 ± 1.95a	17.64 ± 1.11a	17.07 ± 2.52a
Soil total nitrogen (TN, g kg^{-1})	1.43 ± 0.06a	1.28 ± 0.14a	1.01 ± 0.02b
Soil ammonium-N (NH_4^+-N, mg kg^{-1})	8.08 ± 0.24a	7.56 ± 0.31a	5.10 ± 0.35b
Soil nitrate-N (NO_3^--N, mg kg^{-1})	2.32 ± 0.04a	1.88 ± 0.04b	1.65 ± 0.08c
Soil C/N ratio	13.10 ± 0.98b	13.86 ± 1.90ab	16.94 ± 2.83a
Soil pH	4.51 ± 0.04b	4.57 ± 0.02b	4.67 ± 0.04a
Litterfall biomass (g m^{-2} $year^{-1}$)	389.5 ± 13.4a	354.3 ± 9.1a	336.7 ± 7.5b
Litterfall C (g kg^{-1})	483.6 ± 6.89b	508.0 ± 5.06a	509.7 ± 5.90a
Litterfall N (g kg^{-1})	34.2 ± 0.16a	19.2 ± 0.33b	13.9 ± 0.22c
Litterfall C/N ratio	14.13 ± 0.21c	26.49 ± 0.71b	36.67 ± 0.23a
Fine root biomass (g m^{-2})	170.5 ± 15.8a	150.2 ± 10.3a	110.7 ± 8.9b
Fine root C (g kg^{-1})	602.7 ± 8.48a	532.5 ± 9.44b	487.4 ± 7.55c
Fine root N (g kg^{-1})	8.38 ± 0.52a	7.62 ± 0.17b	7.44 ± 0.05b
Fine root C/N ratio	72.6 ± 5.55a	69.87 ± 0.49a	65.54 ± 1.45a
Above-ground C stock (Mg hm^{-2})[A]	18.25 ± 1.08b	27.99 ± 1.02a	28.31 ± 3.35a
Below-ground C stock (Mg hm^{-2})[B]	115.8 ± 5.04a	109.8 ± 3.76ab	102.8 ± 6.72b
System C stock (Mg hm^{-2})[C]	134.1 ± 4.55a	137.8 ± 4.08a	131.1 ± 9.92a

Different lowercase letters indicate significant differences among forest management regimes ($P < 0.05$). Values are mean ± SE ($n = 3$)

[A] Tree + understory + litterfall

[B] From 0 to 100 cm soil layer

[C] Above-ground + below-ground

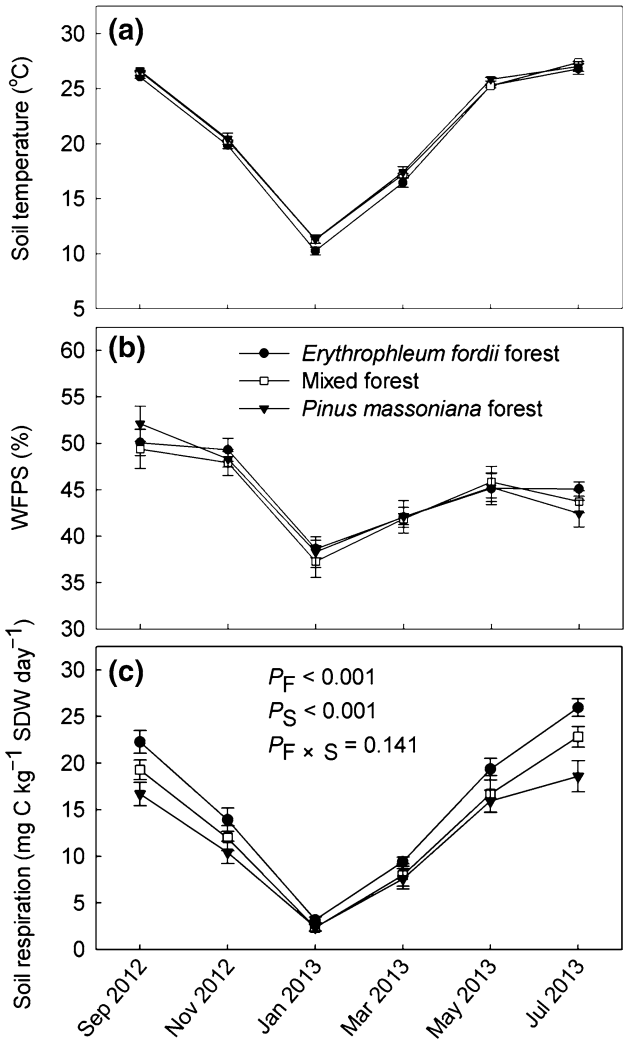

Fig. 1 Dynamics of soil temperature (**a**), water-filled pore space (WFPS), (**b**) and soil respiration (**c**) measured in the three forest management regimes. *SDW* soil dry weight. *Error bars* show standard errors ($n = 3$). P_F, forest management regime effects; P_S, sampling time effects; $P_{F \times S}$, interactions effects of forest management regime × sampling time

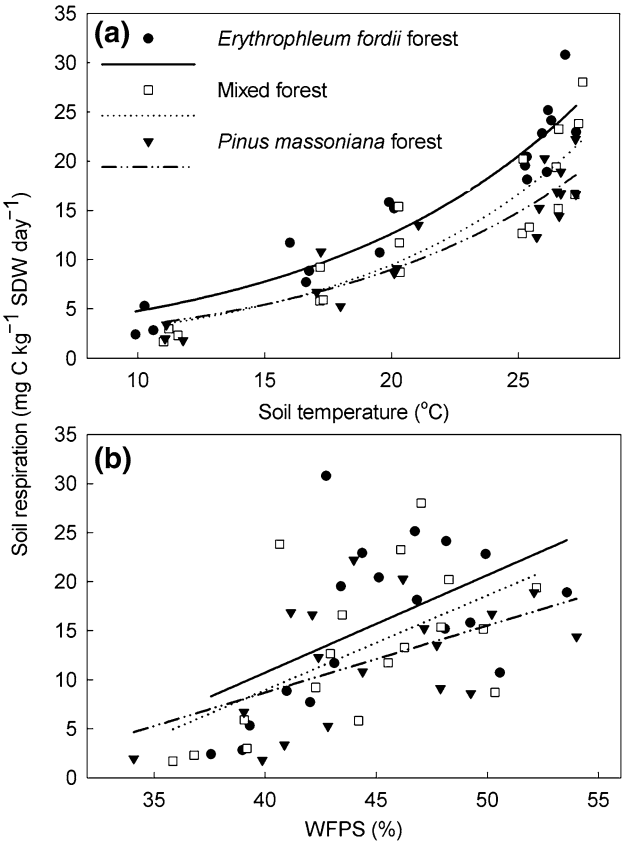

Fig. 2 Relationships between soil respiration and soil temperature (**a**) and water-filled pore space (WFPS), (**b**) in the three forest management regimes

positive bacteria, and gram-negative bacteria significantly increased in *E. fordii* and mixed forest, whereas those of fungal biomass and F/B ratio decreased. Specially, the highest total PLFAs were found in the *E. fordii* forest (11.91 nmol g^{-1}), which were 10.2 % higher than that in the mixed forest (10.81 nmol g^{-1}), and 27.2 % significantly higher than those in the *P. massoniana* forest (9.36 nmol g^{-1}). The bacterial PLFAs, actinomycetic PLFAs, AMF PLFAs, gram-positive bacterial PLFAs, and gram-negative bacterial PLFAs in the *E. fordii* forest increased by 9.7, 12.5, 17.6, 10.3 and 7.7 % compared with those in the mixed forest, respectively, and significantly increased by 33.8, 49.1, 80.3, 34.7 and 31.5 % than those in the *P. massoniana* forest, respectively. However, the fungal PLFAs for the *P. massoniana* forest (1.54 nmol g^{-1}) was higher than that in the mixed forest (1.40 nmol g^{-1}) and significantly higher than that in the *E. fordii* forest (1.24 nmol g^{-1}). The F/B ratio in the *P. massoniana* forest reached the highest of 0.34, which was significantly higher than that in the *E. fordii* forest (0.21) and mixed forest (0.26).

There was no significant relationship between the SOC and all soil microbial PLFAs. Total N and pH were all significantly correlated with all microbial PLFAs except for actinomycetic PLFAs. The C/N ratio was significantly and negatively associated with bacterial PLFAs and actinomycetic PLFAs, but was significantly and positively related with the F/B ratio. The NH_4^+-N and NO_3^--N concentrations were all significantly correlated with all microbial PLFAs except for fungal PLFAs.

Soil microbial community composition

The data concerning the individual relative concentration (mol%) of the 21 most common PLFAs were subjected to a principal component analysis (PCA; Fig. 3). The first principal component (PC1) explained 63.0 % of the total variance in soil microbial communities, while the second, PC2, only explained 19.6 % of the total variance. The PCA biplot revealed that the soil microbial communities from the three forest management re-

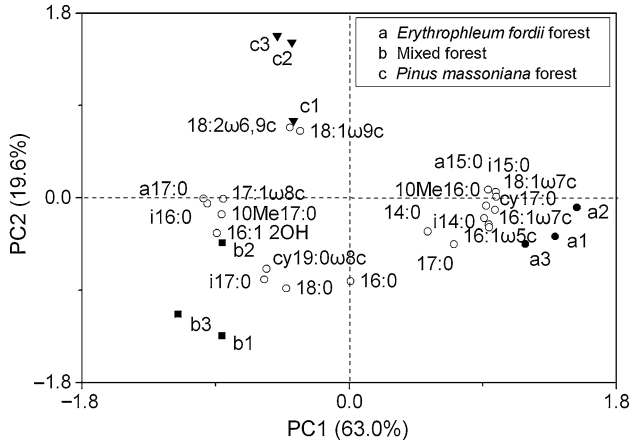

Fig. 3 Principal component analysis (PCA) biplots of the phospholipid fatty acid (PLFA) composition of microbial community in the soil samples from the three forest management regimes. Bacterial PLFAs: i14:0, i15:0, a15:0, i16:0, 16:1ω7c, 17:0, i17:0, a17:0, cy17:0, 18:1ω7c; Actinomycetic PLFAs: 10Me16:0 and 10Me17:0; Fungal PLFAs: 18:1ω9c and 18:2ω6,9c; Arbuscular mycorrhizal fungal PLFA: 16:1ω5c; Other PLFAs: 14:0, 16:0, 18:0, 16:1 2OH, 17:1ω8c, cy19:0ω8c

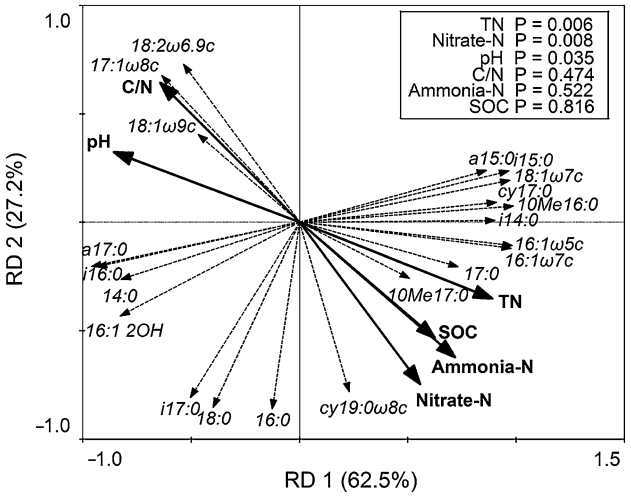

Fig. 4 Redundancy analysis (RDA) of relationships between soil microbial community composition and chemical properties. The *solid lines* represent the soil chemical variables and the *dashed lines* represent the phospholipid fatty acid (PLFA) biomarkers. *SOC* soil organic carbon, *TN* total nitrogen, *C/N* the ratio of soil organic carbon to total nitrogen. Bacterial PLFAs: i14:0, i15:0, a15:0, i16:0, 16:1ω7c, 17:0, i17:0, a17:0, cy17:0, 18:1ω7c; Actinomycetic PLFAs: 10Me16:0 and 10Me17:0; Fungal PLFAs: 18:1ω9c and 18:2ω6,9c; Arbuscular mycorrhizal fungal PLFA: 16:1ω5c; Other PLFAs: 14:0, 16:0, 18:0, 16:1 2OH, 17:1ω8c, cy19:0ω8c. The *P* values presented in figure resulted from the Monte Carlo permutation test

gimes were compositionally distinct from each other. The *E. fordii* forest with higher PC1 scores was observed on the right of the axes 1. By their loading values it is evident that the fatty acids associated with bacteria, including i14:0, i15:0, a15:0, 16:1ω7c, cy17:0, 18:1ω7c, AMF PLFA biomarkers (16:1ω5c), and one of actinomycetic PLFA biomarkers (represented by 10Me16:0) were all most important for the separation of the *E. fordii* forest. The axes 2 separated the *P. massoniana* forest from the other two forest management regimes, and the higher PC2 scores were observed for *P. massoniana* forest on the upper of the axes 2. Specifically, the *P. massoniana* soil was abundant in two fungal PLFAs biomarkers: 18:1ω9c and 18:2ω6,9c (Fig. 3).

Redundancy analysis (RDA; Fig. 4) of relationships between soil microbial community composition and soil chemical properties showed that the first axes (RD1) and second axes (RD2) explained 62.5 and 27.2 % of the total variance of the relationship, respectively. The significance of soil environmental factors (SOC, TN, C/N ratio, NH_4^+-N, NO_3^--N, and pH) present in the ordination was determined by Monte Carlo permutation tests, which demonstrated that the TN ($P = 0.006$), NO_3^--N ($P = 0.010$), and pH ($P = 0.035$) were the key factors in shaping the soil microbial community composition under these forest management regimes assayed in this study.

Relationships between soil respiration and microbial PLFAs

Correlation analysis showed that soil respiration was significantly correlated with the microbial PLFAs of the total, bacteria, actinomycete, AMF, gram-positive bacteria, and gram-negative bacteria ($R^2 = 0.52 - 0.71$, $P < 0.05$ or $P < 0.01$). However, no strong relationship was found between the soil respiration and the fungal PLFAs and the F/B ratio ($P > 0.05$).

Discussion

The temporal and spatial variations of soil respiration in the three forest management regimes in subtropical China were first described. We found that temporal variations of the soil respiration were accompanied by considerable differences in soil temperature as well as soil moisture in all forest management regimes (Figs. 1, 2), indicating that soil temperature and moisture exert crucial effects upon the temporal variations of soil respiration. Similar results were also observed in other forest ecosystems (Tang et al. 2006; Sheng et al. 2010; Wang et al. 2010a). Significant differences in soil respiration have also been observed among different forest management regimes (Fig. 1c). Soil CO_2 emissions from soil respiration primarily generate from heterotrophic (microbial) respiration and autotrophic (root) respiration (Janssens et al. 2001; Shi et al. 2015a). It has been proposed that much of the spatial variations in soil respiration could be explained by differences of soil organic matter, root biomass and soil microorganisms (Ryan and Law 2005; Epron et al. 2006; Sheng et al. 2010; Wang et al. 2010a). The substrate C availability has been reported to have a strong impact on soil respiration or its components (Sheng et al. 2010; Wang

et al. 2013; Shi et al. 2015a). For soil organic C, however, no apparent differences were observed among these forest management regimes in our study (Table 1). Therefore, the observed differences in soil respiration among these particular regimes cannot be directly ascribed to soil organic C. With regard to fine root biomass, it varied significantly with management regime (Table 1). The fine-root biomass in the *E. fordii* and mixed forest was significantly greater than that in the *P. massoniana* forest, indicating that root respiration may be higher in the *E. fordii* and mixed forest compared with that in the *P. massoniana* forest (Yang et al. 2007; Hertel et al. 2009; Sheng et al. 2010). Aside from root biomass, the observed differences in soil respiration in these forest management regimes may be associated with soil microbial biomass. First, there were abundant microbes (e.g., bacteria, AMF and actinomycete) in the *E. fordii* and mixed forest which would potentially contribute to the increase in microbial respiration and thus in soil respiration. Second, soil of *P. massoniana* forest with higher fungal biomass also resulted in lower soil respiration, which might due to fungi incorporating more substrate C into biomass in comparison with bacteria (Sakamoto and Oba 1994; Austin et al. 2004), and the C turnover is generally slower in these ecosystems (Priha et al. 1999; Six et al. 2006). Additionally our correlation analysis also showed that soil respiration was significantly correlated with most of the microbial PLFAs groups. A previous study in a coniferous forest showed that the soil microbial community controls the forest soil respiration, which supported our finding (Wang et al. 2013). An additional factor explaining the relatively low soil respiration in the *P. massoniana* plantation may be partially due to the high C/N ratio of the litter (Table 1). Xu and Hirata (2005) emphasized that litter C/N ratio, as a good indicator of litter quality, is an important factor regulating soil microbial activity and thus influencing soil CO_2 emissions. The previous study showed that tree species with a high litter C/N ratio could decrease soil respiration in subtropical plantations (Wang et al. 2010a). The litterfall C/N ratio was higher in the *P. massoniana* plantation than that in the other two plantations (Table 1), indicating that soil CO_2 emissions may be lower in the *P. massoniana* plantation.

A vast majority of studies have focused on the effects of different forest ecosystems on soil microbial communities (Hackl et al. 2005; Ushio et al. 2008; Lucas-Borja et al. 2012), yet few of them tried to explore the response of soil microbial biomass and community composition to N-fixing tree ecosystems (Boyle et al. 2008; Bini et al. 2013; Hoogmoed et al. 2014b). In the present study, the measured soil total PLFAs from these forest management regimes are roughly comparable to other forest studies (Lucas-Borja et al. 2012), but less than those measured from some tropical and subtropical forests (Bååth and Anderson 2003; Ushio et al. 2008; Cao et al. 2010; Huang et al. 2014), and higher than those of 12 representative natural forests in the eastern part of Austria (Hackl et al. 2005). The observed differences in total PLFAs in different studies possibly arise from some complex factors, such as climate, vegetation composition, temporal and spatial variations in soil characteristics. The forest management with different tree species had different effects on soil microbial community composition, indicating that tree species play an important role in influencing soil microorganisms. Compared with the *P. massoniana* plantation, the monoculture and mixed N-fixing tree plantations increased the soil microbial biomass of different groups. Consistent with our results, Huang et al. (2014) observed similar increases in soil microbial biomass in the 0–10 cm soil within mixed forest of *A. mangium* and *E. urophylla* plantation. Similarly, an earlier study concluded that total microbial biomass as well as actinomycetic biomass in rhizosphere soil in monoculture and mixed culture of legumes were significantly higher than those in non-legumes (Chai et al. 2004). Nevertheless, Boyle et al. (2008) reported that microbial biomass did not vary between *A. rubra* and *P. menziesii* forest soils, where the average N concentrations were 6.3 and 4.7 g kg^{-1}, respectively. It could be speculated that the inherently high soil N status may exceed the threshold for microbial N limitation, consequently may result in no significant response of soil microbes.

In the present study, we found that the soil microbial communities from the three forest management regimes were compositionally distinct from each other (Fig. 3). This could be mainly attributed to the variations of the quality and quantity of litter, soil nutrient availability, and root exudates. Further RDA revealed that the key factors acted on the soil microbial community composition were TN, NO_3^--N and pH (Fig. 4). At least three aspects could be explained for this situation. First, the litters from N-fixing tree species are easily decomposed because of their optimal chemical properties (e.g., high N and low C/N ratio). Therefore, soil organic matter and nutrient input rates and properties would significantly affect soil microbial biomass and community structure (Mendham et al. 2002; Cao et al. 2010). Second, the N-fixing plants might enhance microbial biomass via greater root exudation compared to non-N-fixing plants or specific root exudates from N-fixing plants (e.g., flavonoids) (Martin 1971; Mathesius 2001). Moreover, soil acidification caused by nitrogen fixation and nitrification under N-fixing tree plantations can be responsible for the pH decrease (Yamashita et al. 2008), which further altered the soil microbial community composition. In addition, our study site is located in an area of degraded soil fertility resulting from successive planting of monocultures of coniferous tree species, and the soil has low N content and may be nitrogen-limiting to microbes. However, forest management with N-fixing tree species may alleviate the microbial nitrogen-limitation.

In our study, total PLFAs, which are used to estimate the total microbial biomass, were significantly and positively related to TN, but were not associated to SOC

and C/N ratio, which indicated that TN might account for the variation in total PLFAs. Previous studies also concluded that high soil fertility could stimulate microbial growth in the forest soils (Mendham et al. 2002; Ushio et al. 2008; Wagai et al. 2011). Nevertheless, it was also reported that total PLFAs could be negatively related to SOC and TN (Grayston et al. 2004). Soil types and their associated soil characteristics, such as available phosphorus, pH, texture, and soil moisture has varied in different studies, which might account for the inconsistent relationships between total PLFAs and SOC and TN. Additionally, we found that N-fixing tree plantations increased the bacterial biomass whereas *P. massoniana* plantation increased the fungal biomass. One of the explanations is that the fungi generally have lower N demand (microbial C/N = 4 for bacteria, and 10 for fungi) (Austin et al. 2004), therefore might develop well under N-poor conditions in *P. massoniana* plantation (Carreiro et al. 2000). However, soil nutrients under N-fixing tree plantations provided abundant substrates for bacterial growth, and bacteria adapt to nutrient-rich conditions and use low C/N ratio substrates more efficiently than fungi (Lundquist et al. 1999; Williamson et al. 2005). Another reason for the high prevalence of fungi in the pine *P. massoniana* plantation may be that fungi are presumably more adapted to decompose pine litter as bacteria (Hackl et al. 2005). Pine litter contains a great amount of recalcitrant organic compounds (e.g., lignin and tannins), and fungi are the organisms principally responsible for the degradation of these compounds (Dix and Webster 1995). In addition, low amount of PLFA 16:1ω5c, indicating arbuscular mycorrhizal fungi, may be related to the low but easily utilized soil C in the *P. massoniana* plantation, since a decline in this fatty acid has also been observed after the depletion of easily available C sources in an incubation experiment (Frostegård et al. 1996).

Soil pH is one of the major factors influencing the soil microbial community composition (Frostegård et al. 1993; Bååth and Anderson 2003; Högberg et al. 2007; Lucas-Borja et al. 2012). The observed increase in the total PLFAs with decreasing pH parallels results from Ushio et al. (2008) and Cao et al. (2010). The microbial biomass of AMF, gram-positive and gram-negative bacteria increased with decreasing pH described in our study which is consistent with the results from a tropical montane forest ecosystem (Ushio et al. 2008). It has been proposed that pH is positively related to bacteria and is negatively related to fungi (De Vries et al. 2006; Högberg et al. 2007; Rousk et al. 2009; Lucas-Borja et al. 2012; Dong et al. 2014). One potential explanation for this phenomenon could be that high concentrations of hydrogen ion hinder bacterial growth while low concentrations of hydrogen ion limit fungal growth (Rousk et al. 2009). In our study, however, we found the pH was negatively related to bacteria and a positive correlation was observed to fungi, despite the narrow pH range (Table 1) in our experimental sites. Our findings are contrary to previous studies about the effect of pH on these microbes, and the reason is still unclear.

Conclusions

The inclusions of N-fixing species in forests significantly increased the soil C emission, but have no effects on SOC and ecosystem total C stock. In addition, soil microbial communities were compositionally distinct among the three forest management regimes. Soil total and bacterial PLFAs in the monoculture and mixed N-fixing tree plantations were significantly higher than in the *P. massoniana* plantation, whereas fungal PLFAs were higher in the *P. massoniana* plantation than in the other two plantations. Differences observed in soil microbial community composition were related to the soil chemical properties such as total N, NO_3^--N, and pH. Our study suggests that elevated soil respiration in the N-fixing tree plantations could be primarily explained by the increase of root biomass and soil microbial biomass, but not soil organic carbon. Given that soil fertility and microbial biomass were promoted, forest management with N-fixing trees resulted in no significant increase in ecosystem total C stock but caused further CO_2 production in laboratory assays. The future decision of tree species selection for forest management in subtropical China therefore needs to take into account the potential impacts of tree species on CO_2 emissions.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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